SO_2 POLLUTION. II. INFLUENCE OF INORGANIC SULPHUR COMPOUNDS ON BACTERIAL COMMUNITIES OF FOREST SOILS

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Abstract
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The immission fall-out increases the sulphur content in soils of spruce forests. This leads to an increase of the concentration of thiobacilli, the occurrence of heterotrophic bacteria oxidizing S^0 to SO_4^{2-}, as well as of the incidence of bacteria resistant to sulphite at acid pH. Sulphite acts as an inhibitor or as a stimulator of bacterial growth depending on the pH of the environment. Sulphite in soil is rapidly oxidized to sulphate; various soil heterotrophic bacteria produce sulphite oxidase. Application of compounds from the sulphur cycle into the soil does not evoke changes comparable with those caused by immissions. It seems a proof, that even in soil, sulphur dioxide represents the main noxious factor of the immissions.

The acidification of the environment and its enrichment with sulphur compounds, mainly sulphates, are considered as primary effects of SO_2 immissions on the ecosystem. The negative influences of immissions, especially on the forest ecosystem, are explained mainly by soil acidification (Johnsson, 1976). Experiments carried out with isolated organisms (Wodzinski and Alexander, 1978) and studies of the conditions in polluted localities (Langkramer and Lettl, 1982; Lettl, 1984) showed that environment acidification alone is insufficient for the explanation of the immission effects on the microflora. With certain small definiteness the probable accumulation of toxic products of SO_2 is proposed (Dodd and Lauenroth, 1981). From these compounds, the main attention is paid to sulphite, i.e. a product of hydratation of SO_2.

This work is aimed at an attempt to explain the behaviour of bacterial communities from forest soils under the influence of inorganic sulphur compounds with special respect to sulphite.

Table 1. Average ($\bar{x} \pm S$, (n)) content of sulphate and occurrence of sulphur oxidizers in soils of spruce

Elevation above sea level in m	Locality	Its character	Content of sulphate
			fermentative
500–600	Trstěnice	pure	237 ± 138 (19)
	Šabina	heavy polluted	309 ± 231 (19)
	Hrušková	heavy polluted	383 ± 255 (13)
700–900	Kladská	pure	203 ± 126 (13)
	Prameny	slightly polluted	249 ± 180 (12)
	Nová Ves	heavy polluted	300[a]

[a]One sample taken on 3. 6. 1982.
[b]Analysis of isolates from samples taken on 12.12.1983.

Materials and methods

The localities in the regions Slavkov Forest and Ore Mountain and general methods have been described already (Lettl, 1984).

Results

Enrichment of soil by sulphates

The average numbers content of sulphates in soils of five variously polluted spruce forests in Slavkov Forest during the period 1977—1979 is given in Tab. 1.

Incidence of soil bacteria oxidizing sulphur

The average of chemolithotrophic oxidizers of sulphur (thiobacilli) determined in soil from the fermentative horizons during the period 1977—1979 are shown in Tab. 1.

From the fermentative horizons from soils collected in four spruce growths, 200 cultures of heterotrophic bacteria were isolated, the ability of which to oxidize S^0 to SO_4^{2-} was tested. Table 1 presents the percentage of active cultures from the total number of isolates in individual groups.

Influence of sulphur compounds on microbial conditions in soil

The mixture of fermentative and humus horizons, collected on January 2, 1979 in a spruce growth on an experimental plot belonging to the Institute in Strnady, was filled into polyethylene vegetation containers with a surface area of 110 ×

forest stands

($\mu g \cdot g^{-1}$) in horizons humus	Average numbers of thiobacilli (in thousands per g over dry soil)	Per cent of heterotrophic bacteria[b] oxidizing S^0 to SO_4^{2-} on the medium	
		Thornton, pH 4.0	meat-peptone agar, pH 6.0–8.0
197 ± 98.7 (19)	63.6 ± 82.5 (5)	29.6	45.0
377 ± 238 (19)	398 ± 280 (5)	68.2	80.0
289 ± 132 (13)	283 ± 233 (5)	–	–
120 ± 88.8 (13)	109 ± 63.4 (4)	24.0	52.0
176 ± 147 (12)	10.6 ± 5.6 (4)	–	–
141[a]	4000[a]	59.2	88.0

230 mm and sowed with spruce seeds. The soil was watered twice a week with 100 ml of solution of $Na_2S_2O_3$, Na_2SO_3 and Na_2SO_4 (pH 5.2 to 6.3) in a concentration of 30 µg/ml S. In the course of 14 weeks 84 mg of S on 1 container was supplied by means of 28 waterings. This amount corresponds to an overall fall-off

Table 2. Effect of the supply of sulphur compounds on the properties of spruce forest soil

	Sulphur (84 mg) applied as			Control without S
	$Na_2S_2O_3$	Na_2SO_3	Na_2SO_4	
Content of nutrients				
pH (H_2O)	3.70	3.70	3.80	3.70
pH (KCl)	3.35	3.40	3.40	3.30
NH_4^+–N [$\mu g \cdot g^{-1}$]	373	328	381	374
NO_3^-–N [$\mu g \cdot g^{-1}$]	464	464	479	597
SO_4^{2-} [$\mu g \cdot g^{-1}$]	648	752	313	274
Numbers of microorganisms[a]				
aerobic bacteria	1.4	1.2	1.5	2.1
ammonifying bacteria	1.3	1.1	1.4	2.0
thiobacilli	0.10	0.098	0,099	0.48
microfungi	1.9	1.5	0.93	1.6
Soil biochemical activities[b]				
respiration	765	828	733	1082
ammonification	32.5	46.9	47.7	37.4
nitrification	23.8	12.8	11.3	45.3
oxidation of $S_2O_3^{2-}$	7028	6622	7309	7662
oxidation of S^0	4160	3519	3961	3068

[a]In millions per g over dry soil.
[b]In mg of the reaction product (CO_2, $NH_4^+ - N$, $NO_3^- - N$, SO_4^{2-}, respectively) per kg over dry soil after the incubation: respiration 24 h, $S_2O_3^{2-}$ oxidation 1 week, ammonification and nitrification 2 weeks, S^0 oxidation 3 weeks.

Table 3. Effect of sulphite at different pH on the bacterial populations grown on Thornton agar

pH of the medium	Per cent of colonies[a] grown at the concentration [mM] of sulphite 0		1.0	3.0	10.0	
7.0	100	stimulation	106	350	78	inhibition
6.0	118		117	79	15	
5.0	137		179	71	33	
4.0	256		87	62	29	

[a]Number at pH 7.0 without sulphite = 100 %.

of sulphur in highly polluted localities. Then soil analyses were carried out. The results are summarized in Tab. 2.

The pH-dependent effect of sulphite on the growth of bacterial communities

Thornton's agar with 0, 1.0, 3.0 and 10 mmol/L Na_2SO_3 and with pH within the range of 4.0 to 7.0 was inoculated with soil suspensions from the samples collected from the fermentative and humus horizons on June 3, 1982 in the localities Trstěnice and Nová Ves. The number of developed colonies was evaluated and calculated so that the growth on the medium of pH 7.0 without SO_3^{2-} was considered as 100 %. From the very similar results only the numbers of bacteria in samples from the fermentative horizon collected in Nová Ves are shown in Tab. 3.

The sulphite-resistance of bacteria

Thornton's agar, pH 5.0, containing 0, 1.0, 3.0 and 10.0 mmol/L Na_2SO_3 respectively was inoculated with soil suspensions collected on April 18, 1983 from the fermentative and humus horizons in spruce forests near the villages Kladská, Nová Ves, Trstěnice and Šabina. The numbers of developed colonies were calculated, the growth on the medium without sulphite being considered as 100 % (Fig. 1).

The apical shoots of spruce collected on August 30, 1982 (in the period when maximum development of epiphytic microflora is presumed) in forests near the villages Kladská, Prameny, Šabina and Hrušková, were suspended in 0.15 M NaCl. After 15 min shaking, the suspensions were inoculated on Thornton's agar and further on the same agar medium of pH 4.0 containing 10 mmol/L Na_2SO_3. The numbers of colonies developed on the acid medium with sulphite in Tab. 4 are expressed as a percentage of the number determined on the initial medium without modification.

Oxidation of sulphite in forest soil

Samples of 20 g from fermentative and humus horizons collected in spruce forest on the experimental plot of our Institute in Strnady, were enriched with 5 ml solutions with 500 mg Na_2SO_3 (= 127.8 mg S). At certain time intervals the soil

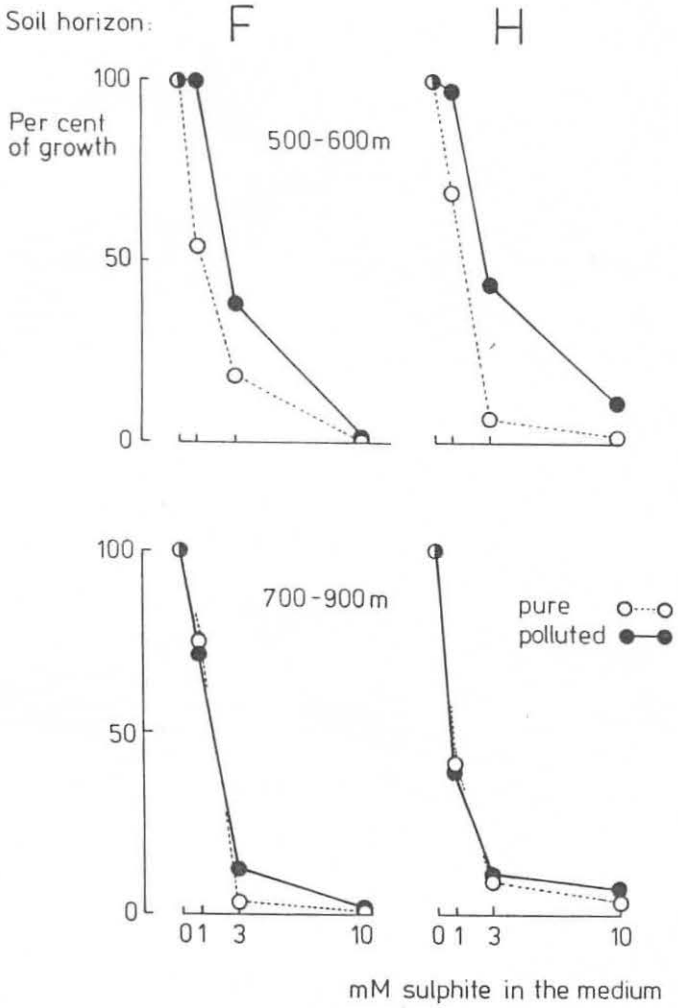

Fig. 1. Relative numbers of bacteria on Thornton's agar (pH 5) containing increasing amounts of sulphite, after inoculation with soil supensions from the fermentative (left) and humus (right) horizons from unpolluted areas (clear points) and polluted areas (black points), at altitudes of 500 to 600 m (above) and 700—900 m above sea level (below).

Table 4. Occurrence of sulphite-resistant bacteria in bacterial populations of spruce phylloplane

Locality	Its character	Per cent of bacteria[a] grown on Thornton agar with 10 mmol/L SO_3^{2-} at pH 4.0
Kladská	pure	0.28
Prameny	slightly polluted	1.55
Šabina	heavy polluted	2.10
Hrušková	heavy polluted	2.85

[a]Numbers of colonies on the Thornton agar without modifications = 100 %.

samples were extracted with water and the concentrations of sulphite and sulphate were determined in the filtrate. The results, expressed as percentage of added S are shown in Fig. 2.

The occurrence of sulphite oxidase activity in soil bacteria

Altogether 74 bacterial cultures were isolated from the samples collected from the fermentative horizon on October 5, 1982 near Nová Ves in a young spruce forest without ground vegetation, in a withered spruce forest with grass undergrowth and in a grassy growth of mountain ash on meat-peptone agar. After 3 days of cultivation on the same liquid medium, the concentration of sulphite oxidase in

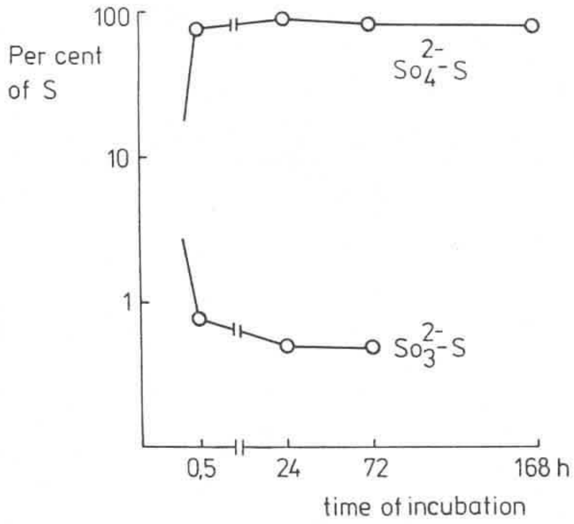

Fig. 2. Changes of sulphite sulphur (127.2 mg sulphite S = 100 %) added to soil from the fermentative horizon.

the culture supernatants was determined. Two cultures from the young spruce forest were active from the total of 24 isolates (8.3 %), in the withered spruce forest 3 cultures from 22 were active (13.6 %) and in the mountain ash growth 7 cultures from 28 isolates were active (25.0 %).

Discussion

By observations in the field (Lochman et al., 1981; Langkramer and Lettl, 1982) as well as by experimental fumigation (Grant et al., 1979b; Dodd and Lauenroth, 1981) it was proved that SO_2 easily decreases the pH, at least of some soil horizons. However, acidification alone does not explain sufficiently the negative impact of immissions on soil microflora (Wodzinski and Alexander, 1978; Lettl, 1984). Accumulation of toxic products of SO_2 (SO_3^{2-}, SO_4^{2-}) in the environment is presumed in this connection (Dodd and Lauenroth, 1981).

Sulphur comes into soil from rain-fall mainly in the form of sulphate (Burns and Galloway, 1981), by direct sorption of SO_2 by soil (Materna and Kohout, 1980) and from litter, which in exposed areas contains higher concentrations of inorganic sulphur (Materna, 1980). Long-term observations of the sulphate content in soil actually prove its higher levels in polluted soils (Tab. 1). Moreover, it seems, that the sulphate content in forest soils exhibits an increasing tendency (Lochman et al., 1981). Similar differences were observed in other regions, too (Pelíšek, 1976; Wainwright, 1978).

Thus, at least a temporary sulphate accumulation in soils can be considered as proved. A partial immobilization of sulphate sulphur occurs in soil (Saggar et al., 1981), which by means of microbial activities is transformed into organic compounds (David et al., 1982) and thus modifies the humus composition: humic and fulvic acids from soils from exposed localities contain twofold amounts of S and N (Kerndorff and Schnitzer, 1979).

This increased content of organic sulphur in soil is a presumption for an increase of the level of other products from the sulphur cycle released during the degradation of organic compounds. In soils from the loaded localities, there were proved to be increased concentrations not only of sulphates, but also of elemental sulphur, thiosulphate and tetrathionate (Wainwright, 1978a). Their origin is ascribed to solid deposits, soot, from which they are released by microbial action (Killham and Wainwright, 1981; Wainwright and Killham, 1982).

Microorganisms respond substantially to this supply of reduced sulphur into soil as to a nutrient: physiological groups of microorganisms able to utilize sulphur are multiplied. Increased numbers of chemolithotrophic thiobacilli were found in soils from the exposed localities. Moreover, among the heterotrophic bacteria from the exposed areas, the number of strains able to oxidize S^0 to SO_4^{2-} doubles (Tab. 1). In some types of growths in polluted regions all isolated cultures of heterotrophic

bacteria possessed this ability. On the contrary, in some regions bacteria with such activity were rare, but their function was taken over by micromycetes. Various microscopic fungi were isolated which oxidized S^0 to sulphate using the polythionate pathway (Wainwright, 1978, 1979; Wainwright and Killham, 1980). Some heterotrophic bacteria can be comparably effective as *Thiobacillus thiooxidans* (Pepper and Miller, 1978), which is considered as a most active oxidizer of sulphur. It seems, therefore, that under the conditions of high amounts of sulphur supply, even heterotrophic organisms together with thiobacilli play a significant ecological role in the sulphur cycle. A great part of the heterotrophic bacteria produces also a thiosulphate sulphurtransferase (rhodanese) (Lettl, 1983a) which so far was considered as a typical enzyme of thiobacilli. In the polluted regions even the ability of soil to oxidize S^0 to SO_4^{2-} increases (Lettl et al., 1981). Thus, it is evident that in exposed localities, at higher levels of sulphur compounds its cycle is intensified. Therefore, all the intermediate products and the fall-out of sulphur can be potentially noxious for the soil microbial community. However, which of these compounds is the actual agent?

Sulphate is considered to be non-toxic (Grant et al., 1979b).

Sulphide or hydrogen sulphide are strongly toxic. In soil rich in sulphur with high water content, such production of sulphide by reduction of sulphate was observed (mainly in the rhizosphere) that plants withered (Dommergues et al., 1969). However, this cannot be the cause in adequately aerated upper horizons of forest soil.

Elemental sulphur was proved as an intermediate product of the cycle in polluted environments (Wainwright, 1978a). Its antibacterial effect was described (Weld and Gunther, 1947), but it was proved that the toxicity was caused by the sulphide formed from it (Woiwod, 1954).

Thiosulphate and tetrathionate can be present in soil environments at relatively high concentrations (Wainwright, 1978a). A certain phytotoxicity of thiosulphate has been described, which, however, could assert its influence only under aseptic conditions and when at least millimolar concentrations were used. Tetrathionate and trithionate were significantly less effective than thiosulphate. The toxicity of thiosulphate disappeared after its application to the soil (Audus and Quastel, 1947). Long-term application of thiosulphate corresponding to the total fall-out of sulphur in strongly loaded localities caused only indistinct nonspecific changes in the microbial community (Tab. 2).

Carbon disulphide can originate by reduction of thiosulphate and tetrathionate in soil rich in organic carbon (Minami and Fukushi, 1981). It seems that insignificant production and high volatility do not permit achieving toxic concentrations of this compoud.

Sulphite: several toxic effects of this anion were described. It inhibits respiration (Grant et al., 1979b), CO_2 assimilation (Hill, 1971) and nitrogen fixation. Its

toxicity increases simultaneously with the effect of NO_2 (Wodzinski et al., 1978). Sulphite reacts nonspecifically with mebrane lipids and proteins and thus damages the structure and the function of cells (Lüttge et al., 1972). Sulphite acts as an inhibitor of several enzymes (Lyric and Suzuki, 1970; Ziegler, 1974).

Studies of its effects on pure cultures of organisms showed that sulphite toxicity is pH-dependent and manifests itself in the acid region (Babich and Stotzky, 1978; Wodzinski et al., 1978). Tab. 3 shows that this dependence on pH takes place also in its effect on the complex population of soil bacteria. It reflects also another fact: low concentrations of sulphite, especially at higher pH, have a markedly stimulatory effect on the bacterial growth — in Tab. 3 it is possible to separate approximately both these effects by a diagonal. Observation of bacterial communities from various localities did not reveal any connection between the immission impact on the areas and a sensitivity of the bacterial communities to the stimulatory effect of sulphite.

It seems possible that sulphite can be considered as the noxiousness only at acid pH. This condition is fulfilled in soil of spruce forests. However, watering of acid spruce forest soil with such an amount of sulphite solution corresponding to the total sulphur fall-out in polluted areas did not prove a distinct effect of sulphite: the numbers of bacteria were decreased but the soil activities from which especially ammonification is very sensitive to immissions, were not affected significantly (Tab. 2). Thus, the influence of sulphite on soil microbial community was non-specific and it did not simulate the actual effect of immissions.

An open question is the possible sulphite concentration which could be present in the exposed soils. The experiment in which the soil was enriched with sulphite, showed that the oxidation to sulphate was very rapid in our case (Fig. 2), in the case of other soils it was only slightly lower (Ghiorse and Alexander, 1976; Grant et al., 1979b) — less than 1 % of the added sulphite remains in soil transitorily. The participation of microorganisms in SO_3^{2-} oxidation is probably small. The process is considered to be mainly abiotic. However, it is not impossible that sulphite oxidase activity proved in various soil bacteria, contributes at least partially to the oxidation. In every case, the instability of SO_3^{2-} in the soil environment decreases the possibility of achieving a toxic level of this anion. However, it was proved experimentally that during 48 h incubation of soil in SO_2 atmosphere, the concentration of SO_3^{2-} increased linearly (Grant et al., 1979b).

It is essential to bear in mind another fact in connection with the previously mentioned findings. By using acid media containing high concentrations of sulphite, it is possible to prove that soil polluted by immissions (especially from lower altitutes of approximately 500 m) contains a higher percentage of bacteria able to develop at toxic levels of sulphite in the medium. This sulphite-resistance was proved not only in soil bacteria (Fig. 1) but also in bacteria colonizing the spruce phylloplane in the polluted areas (Tab. 4). The existence of sulphite-resist-

ant bacteria in the polluted areas can have an anamnestic significance and urges us to admit — even though with hesitation — at least some negative influence of sulphite in the polluted environment.

From the possible inorganic compounds only sulphur dioxide remains. Its high toxicity has been proved in many experiments with pure cultures (Couey and Uota, 1961; Saunders, 1966) and in fumigation experiments with soil. In the latter case, SO_2 inhibited the nitrification (Labeda and Alexander, 1978), production of CO_2 from glucose (Grant et al., 1979a), reduced numbers of bacteria and delayed the degradation of added amino acids (Grant et al., 1979a, b), slowed down the degradation of organic matter and caused a slight acidification of the environment (Dodd and Lauenroth, 1981).

SO_2 penetrates some cm into the soil which absorbs it very eagerly (Materna and Kohout, 1980). Sorption of SO_2 by soil can take place at a significant range: in exposed localities more than 70 % of the sulphur input can be retained by soil in this manner (Nyborg et al., 1976; Jakš, 1983). Therefore, in the exposed field it is necessary to presume oscillating, nevertheless the continuous presence of SO_2 in soil. Its sorption increases with the soil moisture, the toxicity of SO_2 water solution being markedly more toxic than the sulphite solution (Grant et al., 1979b).

It is apparent that by means of SO_2 fumigation of soil it is possible to simulate best the influence of immissions covering the decrease in numbers of bacteria and the reduction of biochemical activities as well as the acidification of the environment. Simultaneously, the conditions for its action in the soil environment are given. Indeed, SO_2 is hydrated in moist environments to sulphite, and thus distinct evidences that the biological effects are actually caused by SO_2 are missing. Nevertheless, in the whole sulphur cycle no other such effective compound was found, the action of which could explain sufficiently the characteristic effects of immissions on soil microflora. It seems reasonable to attribute the main role to sulphur dioxide and perhaps sulphite can participate partially in the process.

Translation submitted by the author

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Lettl A.: **Imise SO_2. II. Vliv anorganických sloučenin síry na bakteriální společenstva lesních půd.**

Imisní spad zvyšuje obsah síry v půdách smrkových porostů. Zvyšuje se koncentrace thiobacilů, výskyt heterotrofních baktérií, oxidujících S^0 na SO_4^{2-}, a výskyt baktérií, rezistentních na sulfit při kyselém pH. V závislosti na pH prostředí působí sulfit jako inhibitor nebo stimulátor růstu baktérií. V půdě se rychle oxiduje na sulfát; řada půdních heterotrofních baktérií produkuje sulfit oxidázu. Aplikace sloučenin z cyklu síry do půdy nevyvolává změny, srovnatelné s vlivem imisí. Zdá se, že i v půdním prostředí je hlavní noxou imisí oxid siřičitý.

Леттл А.: **Имисси SO_2. II. Влияние неорганических соединений серы на бактериальные сообщества лесных почв.**

Имиссийное падение повышает содержание серы в почвах еловых насаждений. Повышается концентрация тиобациллов, появление гетеротрофных бактерий, окисляющих S^0 на SO_4^{2-} и появление бактерий, устойчивых к сульфиту при кислом pH. В зависимости от pH среды воздействует сульфит как ингибитор или стимулятор роста бактерий. В почве он быстро окисляется на сульфат; ряд почвенных гетеротрофных бактерий образует сульфитоксидазу. Применение соединений из круговорота серы в почву не вызывает изменения, сравнимые с влиянием имиссий. Кажется, что и в почвенной среде главной вредной слогающей частью является двуокись серы.